

PRIMARY SETAE AND PORES ON LEGS OF LARVAE OF
NEARCTIC HYDROPORINAE (COLEOPTERA: DYTISCIDAE)

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ABSTRACT

The first instar larvae of 22 North American species of *Hydroporinae* (Coleoptera: Adepaga: Dytiscidae) and one species each of *Amphizoidae* and *Hygrobiidae* were analyzed. The ancestral system of primary setae and pores on the legs of hydroporine larvae was deduced and differences between genera are discussed in a phylogenetic perspective. This system is similar to that described by Nilsson mainly from Palaearctic species except for the addition of one pore dorso-posteriorly on femur of most larval *Hydroporinae* (pore FEa). This addition is suggested since this pore seems homologous to the pore found in larval *Carabidae*, *Amphizoidae*, and *Hygrobiidae*. Such an hypothesis led to suppose that the pore FEa was independently lost within the family *Noteridae*, as well as within the hydroporine genera *Laccornis*, *Liodessus*, and *Desmopachria*. In the light of this work, *Potamonectes griseostriatus* stands out as the species deviating least from the ancestral system proposed for the *Hydroporinae*.

RESUME

Les premiers stades larvaires de 22 espèces nord-américaines d'*Hydroporinae* (Coleoptera: Adepaga: Dytiscidae) ainsi que d'une espèce d'*Amphizoidae* et d'*Hygrobiidae* sont étudiés. Le système ancestral des soies et des pores primaires observé sur les pattes des larves d'*Hydroporinae* est proposé et les différences génériques observées sont discutées d'un point de vue phylogénétique. Le système proposé est semblable à celui développé par Nilsson principalement à partir d'espèces paléarctiques à l'exception de l'addition d'un pore localisé dorso-postérieurement sur le fémur de plusieurs larves d'*Hydroporinae* (pore FEa). Ce pore y est inclus parce qu'il est homologue au pore retrouvé chez les larves de *Carabidae*, d'*Amphizoidae* et d'*Hygrobiidae*. Pareille hypothèse suggère que le pore FEa soit disparu indépendamment dans la famille des *Noteridae* ainsi que chez *Laccornis*, *Liodessus* et *Desmopachria*, trois genres d'*Hydroporinae*. Sur la base de ce travail, *Potamonectes griseostriatus* apparaît l'espèce la plus proche du système ancestral proposé pour les larves d'*Hydroporinae*.

INTRODUCTION

Data about immature stages, particularly in holometabolous insects, are likely to improve adult classifications, since larvae may be considered as different expressions of the same genotype (Bousquet and Goulet, 1984). Each instar thus represents an ontogenetic stage with its own characters, each being important in determining taxa, reconstructing phylogenies, and building classifications.

Bousquet and Goulet (1984) have indicated that the least studied and potentially the most significant set of characters on beetle larvae is that of setae and pores in the first instar and their homologous structures in subsequent instars. They have shown the great stability of these primary setae and pores in carabid larvae.

Few authors have undertaken an analysis of the chaetotaxy of dytiscid larvae. The first real effort to code and name series of sensilla is that of De Marzo (1973) on the mature larva of *Agabus bipustulatus* (L.). Recently, Wolfe and Roughley (1985) have proposed a system for naming sensilla on mouthparts, legs, and urogomphi of the mature larvae of *Matus ovatus ovatus* Leech. This system was modified slightly by Nilsson (1986, 1987a, 1987b) who stressed the highly diagnostic value of secondary leg chaetotaxy in Palaearctic Hydroporinae (including some Holarctic species) and suggested an ancestral pattern of primary setae and pores on the legs of dytiscid larvae (Nilsson, 1988).

The subfamily Hydroporinae is the most diverse subfamily of Dytiscidae with six tribes (eight if the genera *Siettitia* Abeille de Périn and *Pachydrus* Sharp are separated into their own separate tribes), and containing some 75 genera. Adult members of the subfamily are characterized by a number of unique features such as the form of the pro- and mesotarsi which presumably indicate that this subfamily is a monophyletic unit. In addition, one feature is the small size of the individuals. Certain features of the larvae also indicate that the subfamily is monophyletic, the synapomorphy judged the most important being the development of the frontoclypeus into a nasale (Wolfe, 1985).

In contrast to European species, only a small number of Nearctic hydroporine larvae are described. Of the approximately 320 known species, only 41 have larvae and adults associated, and only 10 first instar larvae are actually known. This lack of knowledge may be due both to the difficulty of collecting small larvae and to the problems associated with rearing (Matta and Peterson, 1981).

In a phylogenetic perspective it is useful to study additional taxa and search for new characters in order to increase knowledge about the group in revision and to improve the hypotheses. Given the small number of first instar larvae described, this paper represents the first extensive effort to record and number the primary sensilla of several Nearctic Hydroporinae (including some Holarctic species). The aims of this paper are: (1), to examine the chaetotaxy on the legs of the first instar larvae of Nearctic Hydroporinae, with a special emphasis on Hydroporini, and to propose the ancestral pattern of primary setae and pores for the subfamily; and (2), to classify the generic differences observed into apomorphies and plesiomorphies.

MATERIAL AND METHODS

The notation of primary setae and pores proposed is based on the study of the first instar larvae of 22 species of Hydroporinae belonging to three tribes (six genera) and two species of other families of Hydradephaga, Amphizoidae and Hygrobiidae (Table 1). All the species were reared *ex ovo* except for the out-group families loaned from the Canadian National Collection of Insects (Biosystematic

Table 1. List of the species studied (* = Holarctic species)

Tribe	Species
Hydroporinae	
Bidessini	<i>Liodessus affinis</i> (Say)
Hyphyrini	<i>Desmopachria convexa</i> (Aubé)
Hydroporini	<i>Hydroporus (oblitus) paugus</i> Fall
	<i>Hydroporus (s. str.) badiellus</i> Fall
	<i>Hydroporus (s. str.) columbianus</i> Fall
	* <i>Hydroporus (s. str.) fuscipennis</i> Schaum
	* <i>Hydroporus (s. str.) morio</i> Aubé
	<i>Hydroporus (s. str.) niger</i> Say
	* <i>Hydroporus (s. str.) puberulus</i> LeConte
	<i>Hydroporus (s. str.) signatus</i> Mannerheim
	* <i>Hydroporus (s. str.) striola</i> (Gyllenhal)
	<i>Hydroporus (s. str.) tenebrosus</i> LeConte
	* <i>Hydroporus (s. str.) tristis</i> (Paykull)
	<i>Hydroporus (Neoporus) undulatus</i> Say
	<i>Hygrotus hudsonicus</i> (Fall)
	* <i>Hygrotus impressopunctatus</i> (Schaller)
	<i>Hygrotus laccophilinus</i> (LeConte)
	<i>Hygrotus patruelis</i> (LeConte)
	<i>Hygrotus picatus</i> (Kirby)
	<i>Hygrotus sayi</i> Balfour-Browne
	<i>Laccornis latens</i> (Fall)
	<i>Potamonectes griseostriatus</i> (De Geer)
Hygrobiidae	<i>Hygrobia tarda</i> Herbst
Amphizoidae	<i>Amphizoa</i> sp.

Research Centre). Field collected adults were brought into the laboratory for identification, and placed in breeding containers. Except for some rare species, no food was given to the adults. Hatchlings were isolated and fed with mosquito larvae of an appropriate size.

Legs from both sides were removed and mounted in Hoyer's solution (Barbosa 1974). The structures were examined under a compound microscope.

TERMS

For a better understanding, some of the terms used in the text need to be defined. Most of them have already been discussed by authors studying larval chaetotaxy of insects, but it seems useful to repeat them here.

Sensillum - refers collectively to all socketed chaetotaxal surface structures (Wolfe and Roughley, 1985).

Pore (placoid sensillum) - a minute, generally circular, hole-like (under a compound microscope) sensillum on the cuticle (Bousquet and Goulet, 1984).

Seta - corresponds to a contact receptor (Nilsson, 1988). It is a structure within which the energy of a stimulus arising outside or within the insect is transferred into transmittable information, usually in the form of a nervous impulse (McIver, 1982). This common type of sensillum is elongate, slender, and evenly

tapering. Depending on its form, a seta is spiniform or setiform (hair-like), simple (unifid) or compound (bifid, trifid, *etc.*). Spiniform structures refer to short (approximately equal to or less than two times the maximal width of the tarsal claw) and moderately long seta with the base distinctly enlarged (*e.g.*, the ventral series of the femur (Fig. 1)) as compared to very long setiform seta the base of which is narrower (*e.g.*, setae TR4 and TR7, (Fig. 1)).

Spinula - a non-socketed cuticular structure (Nilsson, 1988) [flat bundles of small setae of Jeppesen (1986)] that occurs on the surface of all segments of the legs. They are usually stronger on the inferior margin of the tibia and the tarsus.

Primary seta and pore - a seta and a pore in the first instar larva and their homologous structure on subsequent instars. As emphasized by Bousquet and Goulet (1984), these are further divided into ancestral (recognized and homologized in most or all the taxa examined) and additional (secondarily evolved).

NOTATION OF SETAE AND PORES

The system used for coding and naming the sensilla is inspired both by Bousquet and Goulet (1984) and Wolfe and Roughley (1985). Setae are coded by two capital letters corresponding to the first two letters of the name of the structure on which the designated seta is located (AB, last abdominal segment; CO, coxa; FE, femur; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter) and a number. Pores are coded in the same manner except that the number is replaced by a lower case letter. The position of the sensilla is described by adding the following abbreviation: A, anterior; D, dorsal; Di, distal; P, posterior; Pr, proximal; V, ventral.

The ancestral system of setae and pores was constructed both by out-group and in-group comparisons. All homologous setae and pores present on the larvae of at least one species of hydroporine studied and on larvae of at least one out-group species (Amphizoidae, Hygrobiidae) was considered as part of the ancestral system. Furthermore, setae and pores on larvae of most species of hydroporine studied were also considered as part of the ancestral system. Homologization has followed the code used by Bousquet and Goulet (1984) for carabid larvae.

RESULTS

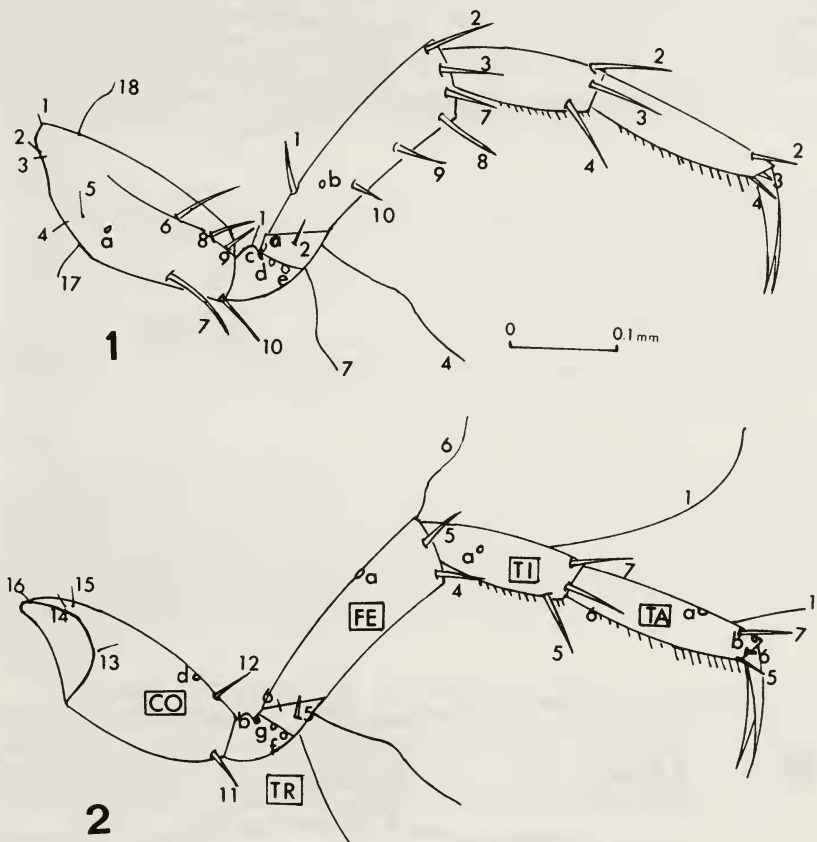
The description of the ancestral systems of primary setae and pores for larval hydroporines refers to a reconstructed species bearing all and only the ancestral setae and pores (Fig. 1-4). Peculiarities of individual species are noted in the text. Except for some few details, the pattern is remarkably constant among all legs and species. Sixty-six sensilla (48 setae and 18 pores) are coded. The position and name of each seta and pore of the ancestral system of legs are listed in Table 2.

Coxa

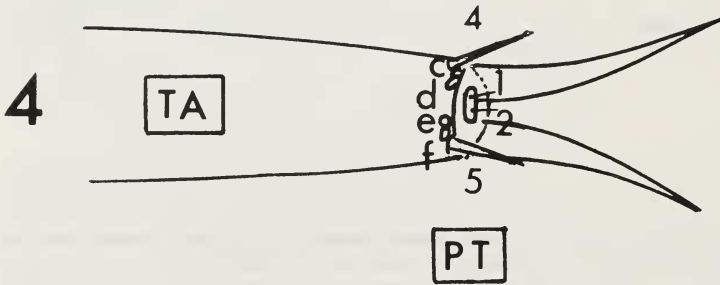
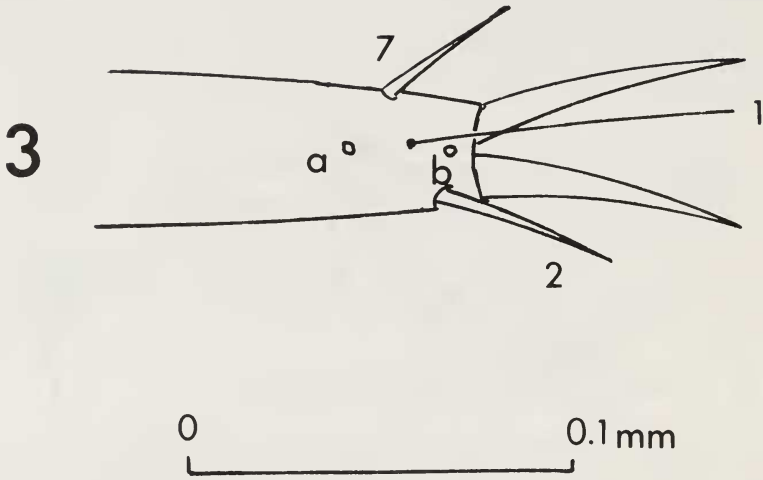
Twenty sensilla are on each coxa. Eleven small setae and one pore appear on the proximal portion of the segment and seven setae and one pore on the distal portion. The setae are spiniform, except CO18, and, in *Desmopachria convexa*, CO12, which are setiform. Seta CO7 is more proximal on the procoxa than on the meso- and metacoxae.

Trochanter

Six setae and seven pores compose the basal number of primary sensilla. These are invariable, with two setiform setae on the ventral margin (TR4, TR7)



Figs. 1–2. Distribution of ancestral setae and pores on hind leg of a generalized first instar larva of Hydroporinae (Coleoptera: Dytiscidae). 1, Anterior face. 2, Posterior face.



Figs. 3-4. Distribution of ancestral setae and pores on hind leg of a generalized first instar larva of Hydroporinae (Coleoptera: Dytiscidae). 3, Dorsal face of tarsus. 4, Ventral face of tarsus (with pretarsus).

and four short spiniform setae. Seta TR5 is more robust consistently than any other seta of the trochanter. All spiniform setae are simple except in first instar larvae of *Desmopachria convexa*, *Hydroporus (Neoporus) undulatus*, *Hydroporus (s. str.) tenebrosus*, *H. (s. str.) striola*, *Hygrotus sayi*, and *H. patruelis*, where TR5 is a compound spine on the posterior surface. Seta TR2 is absent consistently from first instar larvae of *Desmopachria convexa*, *Liodessus affinis*, *Hydroporus (Neoporus) undulatus*, and all species of *Hygrotus* examined. Seta TR2 is facultative in *Laccornis latens* being either present, partially present or absent. Observations of third instar larvae of this species have shown that this seta is constant, and therefore is incorporated into the ancestral system.

Femur

Ten setae and two pores characterize this segment. All setae are spiniform except the setiform FE7 on the distal portion of the superior margin. Most of the spiniform setae are compound in first instar larvae of *Desmopachria convexa*, *Liodessus affinis*, and all *Hygrotus* and *Hydroporus* species. Pore FEa is absent from those of *Laccornis latens*, *Desmopachria convexa*, and *Liodessus affinis*. Setae FE7 is slightly more ventral in position on the profemur than on the meso- and metafemora. Two additional setae, ADi (*H. puberulus*, *H. columbianus*, and *H. tenebrosus*) and AVPr (*L. affinis*), were sporadically noted in some specimens.

Tibia

Seven setae (six spiniform and one setiform) and one pore are on the tibia. First instar larva of *Desmopachria convexa* is characterized by a setiform seta TI7. The inferior margin of the segment is usually marked by a pronounced thickening of the spinulae on the inferior margin. This spinular row is lighter in *Desmopachria convexa*, *Liodessus affinis*, and *Hydroporus paugus*. Compound spines are observed among the same species as above (see femur).

Tarsus

Seven setae (six spiniform and one setiform) and six pores are on the tarsus (Fig. 1-4). Setae TA3 and TA6 are short and robust. The individual pores of the pairs TA_c/TA_d and TA_e/TA_f are very difficult to distinguish in some taxa because they are positioned close together (Fig. 4). The spinular row is markedly developed in larvae of most species except those of *Desmopachria convexa*.

Pretarsus.

Two short spiniform setae are located distally on the ventral surface of the pretarsus (Fig. 4). These may be overlooked easily and incorporated into the row of spinulae of the tarsus.

COMPARISONS AND TAXONOMIC IMPLICATIONS

Except for a few details, the ancestral system of the larval leg of Nearctic Hydroporinae is similar to that described by Nilsson (1988). Differences in the nomenclature of the sensilla (marked by an asterisk in Table 2) are a matter of interpretation rather than of taxonomic difference except for the pore FEb that corresponds apparently to the pore FEa of Nilsson. By comparison with the ancestral pattern of Carabidae, Nilsson's description of pore FEa (APr, antero-proximal) seems much more like pore FEb (LAB, lateral-anterior-basal) than FEa (DB, dorsal-basal).

Table 2. Position of ancestral setae and pores on legs of first instar larvae of Hydroporinae; A - anterior, CO - coxa, D - dorsal, Di - distal, FE - femur, P - posterior, PT - pretarsus, Pr - proximal, TA - tarsus, TI - tibia, TR - trochanter, V - ventral. [* different from Nilsson's (1988) codes].

Setae or pores	Position	Setae or pores	Position
CO1	DPr	TI1	DDi
CO2	ADPr	TI2	ADDi
CO3	ADPr	TI3	ADi
CO4	APr	TI4	AV
CO5	APr	TI5	PV
CO6	A	TI6	PDi
CO7	AV	TI7	PDDi
CO8	ADi	T1a	P
CO9	ADi		
CO10	AVDi	TA1	DDi
CO11	PVDi	TA2	ADDi
CO12	DDi	TA3	ADi
CO13	PPr	TA4	AV
CO14	PDPPr	TA5	PV
CO15	PDPPr	TA6	PDi
CO16	DPr	TA7	PVDi
CO17	VPr	TAa	D
CO18	ADP	TAb	DDi
COa	*APr	TAc	AVDi
COb	DDi	TAd	AVDi
		TAe	PVDi
		TAf	PVDi
TR1	D		
TR2	ADi		
TR4	VDi	PT1	AVDi
TR5	PDi	PT2	AVDi
TR6	PDi		
TR7	V		
TRa	*ADDi		
TRb	*D		
TRc	AD		
TRd	A		
TRe	A		
TRf	P		
TRg	P		
FE1	DPr		
FE2	ADDi		
FE3	ADi		
FE4	PVDi		
FE5	PDi		
FE6	DDi		
FE7	AVDi		
FE8	AV		

(continued on next page)

Table 2. (continued)

Setae or pores	Position	Setae or pores	Position
FE9	AV		
FE10	AVPr		
FEa	*P		
FEb	*APr		

Table 3. Differences in the character states of primary setae and pores on larval legs of selected genera of Nearctic Hydroporinae; (0) plesiotypic state, (1) apotypic state, (a) *Laccornis*, (b) *Desmopachria*, (c) *Liodesus*, (d) *Hydroporus s. str.*, (e) *Hydroporus (oblitus group)*, (f) *Hydroporus (Neoporus)*, (g) *Hygrotus*, (h) *Potamonectes*.

Character states	a	b	c	d	e	f	g	h
1- CO12 spiniform	0		0	0	0	0	0	0
CO12 setiform		1						
2- TI7 spiniform	0		0	0	0	0	0	0
TI7 setiform		1						
3 TR2 present	0			0	0	0		
TR2 absent	1	1		1	1			
4- FEa present				0	0	0	0	0
FEa absent	1	1	1					
5 setae simple	0							0
setae compound	1	1	1	1	1	1		

Table 3 summarizes the differences in the character states for the primary chaetotaxal pattern among genera of the Hydroporinae studied. Character states are presented here as plesiomorphic and apomorphic to underline apparent evolutionary tendencies, but these should be considered first order hypotheses. Because of the large number of genera in this subfamily, a comprehensive treatment should incorporate a larger number of species of a variety of genera and a larger number of characters.

The presence or absence of seta TR2 represents an interesting diagnostic character. Nilsson (1988) noticed that this seta is absent from the legs of Bidessini (*Bidessus* Sharp, *Yola* Des Gozis), *Hydrovatus* Motschulsky, *Hyphydrus* Illiger, and *Hygrotus* Stephens. If the absence of this seta from the legs of species of Nearctic representatives of *Hygrotus* is consistent with Nilsson's data, it is interesting to include in the group of hydroporine genera without TR2 some

strictly Nearctic lineages such as *Desmopachria* and *Liodesus*, and the subgenus *Neoporus* (*Hydroporus*). The absence of TR2 from the trochanter of third instar larvae of *Hydroporus* (*Neoporus*) *carolinus* (unpublish. data) reinforces the hypothesis that this seta is absent from all the species of *Neoporus*. Considering that until now a generic distinction among Nearctic *Hygrotus* and *Hydroporus* based on larval characters was not possible (Watts, 1970; Matta, 1983), it is noteworthy that, except for the subgenus *Neoporus*, the first instar larva of all the *Hydroporus* species studied can be discriminated from the first instar larva of the species of *Hygrotus* by the presence of this seta.

Larvae of *Desmopachria convexa* deviate farthest from the ancestral pattern. The setiform aspect of seta T17 associated with the absence of seta TR2 and pore FEa is similar to that described for larvae of *Hyphydrus* species studied by De Marzo (1977) and Nilsson (1988). The similarities in the basal pattern of both genera are interesting given that Young (1980) and Biström (1982) have suggested that *Desmopachria* and its relatives should be removed from Hyphydrini and placed in a distinct tribe.

The only fundamental difference between the basal pattern proposed herein and that of Nilsson (1988) is incorporation of pore FEa (as defined in this paper) into the ancestral system of larvae of Hydroporinae. Two different hypotheses may be examined with respect to this pore. Hypothesis 1 is that the pore is part of the ancestral system of larvae of Dytiscidae and also of Hydroporinae since it seems homologous to the pore found in most larvae of Hydroporinae as well as in larval Carabidae (Bousquet and Goulet, 1984), Amphizoidae, and Hygrobiidae. There are certainly various interpretations of Adephagan phylogeny but if we accept the idea that Dytiscidae have evolved from a terrestrial carabid ancestor (Hammond, 1979; Ward, 1979; Nichols, 1985), and, even if this is more contested, that Trachypachidae, Dytiscidae, Amphizoidae, Hygrobiidae, and Noteridae could represent a monophyletic unit (Beutel and Roughley, 1988), it seems reasonable to accept pore FEa of the Hydroporinae as ancestral. Based on immature characters, the work of Ruhnau (1986) reinforces this hypothesis since he has shown that Amphizoidae, Hygrobiidae, and Dytiscidae share numerous striking synapomorphies. As a result, hypothesis 1 suggests that pore FEa was independently lost from Noteridae, as well as from *Laccornis*, *Liodesus*, and *Desmopachria*.

Hypothesis 2 is that pore FEa is not part of the ancestral pattern of either Hydroporinae or Dytiscidae. This appears to be the premise of Nilsson (1988) which is supported by the absence of this primary pore in first instar larvae of Haliplidae, Noteridae, and Gyrinidae and by the phylogenetic hypothesis that Noteridae are the sister-group of Dytiscidae (Kavanaugh, 1986). Such a viewpoint suggests thus that the presence of this pore in exactly the same position by larvae of independent families of Adephaga [as well as in most Dytiscidae (Nilsson, 1988)] could result from independent gains.

From both hypotheses, hypothesis 1 appears more acceptable since it seems more logical that pore FEa was lost independently rather than gained independently. In the light of this hypothesis, *Potamonectes griseostriatus* stands out as the species deviating least from the ancestral system proposed for the Hydroporinae. Nilsson (1988) has emphasized that the Holarctic *Laccornis oblongus* Stephens should present the most plesiomorphic condition within Hydroporinae and this is in accord with the previous conclusion of Wolfe (1985). The pattern of primary setae and pores of *Laccornis latens* could also be used as an argument to consider that FEa is an additional rather than an ancestral pore. In order to solve this apparent contradiction, additional larval characters are needed. A

study of the primary setae and pores of other structures such as those of the last abdominal segment and the urogomphi may assist in resolving this controversy.

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